

Geographic variation in the Malagasy Scops-Owl (*Otus rutilus* auct.): the existence of an unrecognized species on Madagascar and the taxonomy of other Indian Ocean taxa

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The taxon *Scops madagascariensis* was one of several apparently new mammals and 14 bird species for which A. Grandidier sent scientific descriptions by letter from Madagascar that were published in March 1867 (Grandidier 1867a). However, by June of that year Grandidier had learnt of senior synonyms for seven of his new birds (Grandidier 1867b). Two scops-owls had previously been reported from Madagascar (Kaup 1852, Hartlaub 1861): a brown one, now Sulawesi Scops-Owl *Otus manadensis* (Quoy & Gaimard 1830) and a rufous one, now Malagasy Scops-Owl *Otus rutilus* (Pucheran 1849a); Grandidier synonymised his *Scops madagascariensis* with the former. He then (Grandidier 1867c) followed Schlegel (1866) in listing *rutilus* as a synonym of *manadensis* as well. Since then, only one scops-owl taxon has been formally recognized in Madagascar, and it now is accepted that *rutilus* and *manadensis* (the latter of the Sulawesi region) are separate species.

More recently, it has also become evident that marked differences exist between the songs of scops-owls in eastern and western Madagascar, roughly corresponding to the wet and dry zones, respectively (G. S. Keith, in Marshall 1978; Goodman *et al.* 1997). Recent publications have mentioned the possibility of a second scops-owl in Madagascar based largely on this geographical trend in song (Morris & Hawkins 1998, König *et al.* 1999, Marks *et al.* 1999), but only weak morphological correlates to song type, in the form of a tendency to be more rufescent in the east and greyer in the west, had been recognized (Benson *et al.* 1976, Marshall 1978, Sinclair & Langrand 1998). We examined geographic variation in morphology and vocalizations of the Malagasy Scops-Owl in order to determine whether more than one taxon was involved on Madagascar and how many biological species should be recognized on islands in the western Indian Ocean.

Methods

Specimens of the following taxa (all of which have sometimes been considered conspecific) were studied: Malagasy Scops-Owl, *Otus r. rutilus*, *sensu lato* (hereafter *s.l.*; n = 141), the Mayotte Scops-Owl *O. [r.] mayottensis* (n = 10), the Moheli Scops-Owl *O. moheliensis* (n = 3), the Anjouan Scops-Owl *O. [r.] capnodes* (n = 47), the Grand Comoro Scops-Owl *O. pauliani* (n = 1), the Pemba Scops-Owl *O. pembaensis* (n = 6), and the Seychelles Scops-Owl *O. insularis* (n = 7). In the following, *O.*



Plate 1. The Torotoroka Scops-Owl *Otus madagascariensis* (upper four, from left to right: grey morph, reddish-brown morph, dark brown morph, and grey morph; all adults), with the Rainforest Scops-Owl *Otus rutilus* (lower four, from left to right: two rufous morph adults, dark brown morph adult, and a grey morph immature). Original painting by Ian Lewington.

rutilus (if unqualified) refers to the species *sensu strictu* (the primarily eastern form), *O. rutilus (s.l.)* is used where the two Madagascar forms were not distinguished. For *moheliensis*, *capnodes*, *pauliani*, and *pembaensis*, all published specimens were examined. Measurements (for consistency, all taken by PCR) were: culmen length from skull base; depth of upper mandible at distal edge of cere; length of straightened 'eartuft'; length of flattened wing (maximum length, Svensson 1970); shortfalls of each primary from the wingtip (the primaries numbered ascendantly, with P1 the outermost, as in Svensson 1970); length of P1 from the smaller overlying under primary coverts; tail length from insertion point between the central rectrices; tail graduation as the distance between the tips of the longest (central, R1) and the shortest (outermost, R6) rectrices; tarsus length (by the standard method in Svensson 1970); minimum width of the tarsus; greatest distal tarsus width; lengths of middle claw and hindclaw from the distal scute, and middle claw depth at the same point; lengths of longest (straightened) rictal bristle and distal extension of the auriculars measured from the bases; length of unfeathered front tarsus measured from the tip of the most distal feathers to the middle of the joint between the first and second digits of the middle toe (used because this joint is normally prominent on specimens); rear tarsal feathering measured from the point at which feathering is complete around the back to the base of the hallux (although this landmark is more proximal than is the anterior landmark); approximate widths of pale and dark tail bands (measured where band widths are about average) on the midsections of the central rectrices. Percent of tarsus feathered = (tarsus length - front unfeathered length) + (tarsus length - rear unfeathered length) / 2 / tarsus length. Statistics were computed using SYSTAT. Univariate statistics, Principal Components Analyses (PCAs), and Discriminant Functions Analyses (DFAs) were done using untransformed data. For PCAs, correlation matrices were used, and mean group factor scores were tested using two-sample *t*-tests. For adults, five plumage characters (overall colour, prominence of facial disk rim, degree of streaking on back, coarseness of underparts barring, and prominence of banding on upper surface of rectrices) were scored from 1 (*rutilus*-like) to 4 (*madagascariensis*-like), and were tested for significance using Kruskal-Wallis one-way analyses of variance.

For comparative purposes, many photographs were taken of nearly all specimens examined for this study and their labels. Localities and relevant details for specimens used in the analyses are given in Appendix 1. A few specimen localities were illegible or untraceable, and many specimens are simply labelled 'Madagascar'; all these were excluded from analyses. Specimens known to have been collected in a general part of Madagascar, either by regional label annotations or by association with a collector who operated only in that region, were included in statistical analyses when possible but were not mapped. Specimen identifications were done by PCR. Full names of museums for which acronyms are given in the text are presented in the Acknowledgements.

Tape recordings of *Otus rutilus (s.l.)* from all major regions of Madagascar were made by TSS and AFAH (Appendix 2). A few additional recordings from other field

observers complemented our geographic sampling. None of the recordings were of birds that were subsequently collected, so the sex of all the tape-recorded birds is unknown. TSS used Canary 1.2.4 (Bioacoustics Research Program, Cornell Laboratory of Ornithology) to analyze his recordings and recordings submitted to him. Default settings for Canary were used except for the display style of sonagrams (smooth rather than boxy) and the overlap was set at 96.88%. One song per song bout was selected for quantitative analysis; the selection was based on loudness of the song, regardless of whether the song was recorded under 'natural' conditions or following tape playback. The variables measured were: number of phrases per song; number of notes per phrase; length of the interval between phrases; length of each phrase in the song; and lowest (F_{\min}) and highest (F_{\max}) frequency of each harmonic of each phrase. AFAH and RV used Avisoft (Ranft 1995; Specht 1999, Avisoft-SAS, Lab Pro 3.73, Berlin, Germany), and their statistics differ only in that they did not discriminate between harmonics when recording F_{\min} and F_{\max} .

Results

A suite of plumage and mensural characters, in combination, distinguish almost all scops-owls from eastern and northern rainforest Malagasy localities from those of western and drier forest areas. This non-clinal variation correlates strongly with song type, and it is therefore necessary to recognize a second species of scops-owl in Madagascar. To facilitate reference for the rest of this paper, we deal first with the nomenclature, and then provide corroborative data for morphology and vocalizations.

As detailed below, *Otus rutilus* (Pucheran 1849) clearly applies to the eastern form, while *Otus madagascariensis* (Grandidier 1867) definitely pertains to the western form. Although *Otus madagascariensis* Smith, 1834 was the original name for the Madagascar Long-eared Owl *Asio madagascariensis*, this and *Scops madagascariensis* have never been placed within the genus *Otus* contemporaneously, so the name *Otus madagascariensis* (Grandidier 1867) is available for, and must henceforth be applied to, the species of scops-owl primarily inhabiting western Madagascar.

Differential diagnoses of *Otus madagascariensis* and *Otus rutilus*

As the original descriptions of both *rutilus* and *madagascariensis* are very brief and do not distinguish between these taxa, we provide amended differential diagnoses below. All characters given below are somewhat variable, but each holds for most specimens, and in combination nearly all specimens can be confidently identified. The characters are those of full adults unless specifically noted.

Otus madagascariensis, like *O. rutilus*, is a medium-sized scops-owl with variable plumage, but the former occurs predominantly in finely vermiculated greyish to yellowish-brown morphs (61.3%, $n = 44$), while *rutilus* occurs mainly in saturated rufous and dark rufescent brown morphs (88.3%, $n = 77$) (Plate 1, Fig. 1). Rarely, *madagascariensis* occurs in a rufous morph (4.5% of the sample), but this is rather



Fig. 1. Scores for qualitative morphological characters of adults of *Otus rutilus* and *O. madagascariensis* mapped against vegetation zones (after Rand 1936; black = rainforest, diagonal hatching = deciduous and dry forest, grey tone = subdesert, white = mainly treeless habitats). Characters were scored from 1 (*rutilus*-like) to 4 (*madagascariensis*-like), and increasing scores are represented by increasing darkness of squares. From left to right for each locality, characters represented by squares are: overall colour (rufous to grey); facial disk rim (obsolete to prominent); mantle streaking (obsolete to prominent); coarseness of cross-barring of underparts (coarse to fine); and tail banding (vague to prominent). Site numbers are on the left of each bar and n for that site on the right. Summary statistics for each locality are provided in Table 4, and localities and associated data are listed in Appendix 1.

pale and orange overall, and retains streaking on the upperparts and white barring on the underparts, while rufous morph *rutilus* are usually rich, dark rufous overall, with obsolete markings.

Otus madagascariensis has less conspicuous whitish supercilia than does *O. rutilus*; its ear tufts are slightly shorter and typically appear prominent because the surrounding feathers are relatively short and compact; its facial disk is nearly uniform in colour but slightly paler near the posterior edge and with a more prominent black rim; its rectal bristles and distal extensions of the auriculars are less profuse, and the longest of these average shorter (Table 1).

The mantle of *Otus madagascariensis* has a relatively solid, paler background colour overlain with long, fairly prominent streaks (Fig. 1, Table 3), while that of *O. rutilus* is typically darker, often with many paler spots, and usually unstreaked or with inconspicuous streaks. The underparts of *madagascariensis* have long thin vertical blackish streaks overlying a finely vermiculated transverse pattern in which white bars are scarcely apparent, and the ground colour contrasts little with scattered white patches of the lower underparts, while the underparts of *rutilus* typically have coarser, shorter blackish streaks overlying a dark background colour with broader, more obvious white cross-bars, and with strongly contrasting scattered white patches on the lower underparts.

In both taxa, the lower scapulars are white with small triangular black tips and usually some fine black subterminal patterning, and the remiges have broad dark and narrower whitish banding. In *madagascariensis*, the tail is relatively long (Table 1) and more graduated, with prominent broad dark bands and narrower pale bands that typically lack rufescence, while *rutilus* has a shorter, squarer tail that is usually weakly banded, often strongly rufescent, and with the dark bands narrower. The wing/tail ratio is lower in *madagascariensis* than for *rutilus* due to the longer tail but similar wing length of the former (Table 1). The tertials of any given specimen are typically banded very like the uppertail surface, and thus those of *madagascariensis* are usually more heavily banded than those of *rutilus*.

Otus madagascariensis has the tarsi heavily feathered, almost to the tarsal joint on the anterior (front) surface and along most of the plantar (rear) edge (Table 1, Fig. 2), and the tarsal feathering is fairly full and dense. In *O. rutilus*, the tarsus is less extensively feathered anteriorly, and much or all of the rear edge of the tarsus is usually unfeathered; the tarsal feathering appears shorter and rather scanty. Both species have moderate-sized, mostly dark bills, narrow pinkish orbital skin, yellow irides, and pale greyish toes, but the claws of *madagascariensis* appear mostly dark in dried specimens and average larger, whereas the smaller ones of *rutilus* appear mostly pale.

Immature *madagascariensis* closely resemble adults in plumage, with perhaps an even more strongly banded uppertail surface, but they are best distinguished on the basis of the narrower, more pointed tips to their rectrices. Immature *rutilus* differ additionally and more obviously from adults (and resemble all ages of *madagascariensis*) in having more prominently banded central rectrices, usually more



Fig. 2. Scores for quantitative morphological characters of adults of *Otus rutilus* and *O. madagascariensis* mapped against vegetation zones (as in Fig. 1). In order, from left to right, characters are: wing/tail ratio (white > 2.2, black < 1.7); percent of tarsus feathered (white < 45%; black > 85%); Factor 1 scores from PCA (white < 1.5; black > 1.5); and scores from DFA (white < 3.0; black < -3.0). Summary statistics for all data are presented in Tables 1 and 2.

TABLE 1. Summary statistics (mean \pm s.d., *n*) for measurements of *Orus madagascariensis*, *O. rutilus*, Comoran taxa, and *O. pumbaensis*. Full adults only were used for *madagascariensis* and *rutilus*, while birds in first basic plumage are included for the other taxa. L = length, d = depth, w = width, s = shortfall from wingtip. Significance levels (ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$) between *madagascariensis* and *rutilus* (listed after *madagascariensis*) are from two-sample t-tests with separate variances.

Variable	<i>madagascariensis</i>	<i>rutilus</i>	<i>mayottensis</i>	<i>capoides</i>	<i>moheliensis</i>	<i>pailliani</i>	<i>pumbaensis</i>
Culmen l	20.5 \pm 0.8, 31 ns	21.0 \pm 0.8, 58	25.7 \pm 0.4, 8	22.5 \pm 1.1, 23	24.0 \pm 1.6, 3	19.9	21.4 \pm 0.9, 6
Maxilla d	7.2 \pm 0.5, 32 ns	7.2 \pm 0.4, 57	8.2 \pm 0.4, 9	8.0 \pm 0.4, 25	7.9 \pm 0.5, 3	6.3	7.6 \pm 0.3, 6
Tuft 1	26.0 \pm 2.5, 31***	28.1 \pm 2.3, 57	27.8 \pm 1.4, 10	29.2 \pm 2.6, 17	26.2 \pm 1.7, 3	25.0	24.7 \pm 1.0, 6
Wing l	156.4 \pm 4.4, 31 ns	156.1 \pm 5.2, 57	170.4 \pm 2.9, 10	163.9 \pm 2.8, 25	164.3 \pm 4.5, 3	140/144 ⁴	151.5 \pm 2.7, 6
P1 s	41.7 \pm 2.5, 14 ns	42.0 \pm 3.7, 43	43.0 \pm 2.2, 9	41.2 \pm 3.4, 25	40.0 \pm 3.0, 3	37	33.5 \pm 2.3, 6
P2 s	17.2 \pm 1.6, 15 ns	17.7 \pm 2.4, 41	17.9 \pm 1.4, 9	15.9 \pm 2.4, 24	15.3 \pm 2.5, 3	16	11.0 \pm 1.8, 6
P3 s	5.2 \pm 1.1, 15 ns	5.4 \pm 1.3, 41	5.4 \pm 1.8, 10	3.8 \pm 1.3, 24	5.7 \pm 1.1, 3	1	2.1 \pm 0.5, 5
P4 s	0.2 \pm 0.4, 15 ns	0.2 \pm 0.5, 42	0.1 \pm 0.3, 10	0.3 \pm 0.6, 24	0.0 \pm 0, 2	0	0 \pm 0, 6
P5 s	1.0 \pm 0.7, 15 *	0.5 \pm 0.7, 40	1.1 \pm 0.9, 10	0.8 \pm 0.9, 24	0.0 \pm 0, 3	0	1.6 \pm 0.9, 6
P6 s	6.2 \pm 1.4, 15 *	5.1 \pm 1.3, 41	6.5 \pm 1.4, 10	4.7 \pm 1.9, 24	6.2 \pm 1.6, 3	11	7.0 \pm 0.6, 6
P7 s	12.1 \pm 1.8, 15 ns	11.8 \pm 2.0, 41	13.5 \pm 1.6, 10	11.8 \pm 2.5, 24	16.3 \pm 2.3, 3	15	12.8 \pm 1.2, 6
P8 s	20.1 \pm 2.0, 15 ns	19.2 \pm 2.5, 40	21.3 \pm 1.5, 10	19.9 \pm 3.7, 24	22.7 \pm 1.1, 3	-	19.3 \pm 1.6, 6
P9 s	26.8 \pm 1.9, 15 ns	26.0 \pm 2.6, 40	27.7 \pm 1.7, 10	27.2 \pm 3.7, 24	30.0 \pm 1.0, 3	-	26.5 \pm 2.3, 6
P10 s	32.9 \pm 2.4, 15 ns	33.0 \pm 3.2, 40	36.3 \pm 2.7, 10	35.3 \pm 3.5, 24	36.7 \pm 1.1, 3	-	32.3 \pm 2.7, 6
Primary 1 l	71.3 \pm 4.6, 28 *	68.9 \pm 4.5, 51	78.5 \pm 3.3, 9	78.5 \pm 3.9, 21	74.7 \pm 3.2, 3	64	69.8 \pm 4.2, 6
Tail l	84.8 \pm 3.0, 25 ***	78.7 \pm 3.8, 54	83.3 \pm 3.1, 9	82.7 \pm 2.5, 19	83.0 \pm 1.0, 3	71/73 ⁵	75.0 \pm 1.6, 6
Tail graduation	10.3 \pm 1.7, 25 ***	8.1 \pm 2.1, 48	6.5 \pm 1.2, 9	6.6 \pm 2.6, 14	7.8 \pm 1.6, 3	0	8.8 \pm 2.4, 6
Tarsus l	30.4 \pm 1.2, 30 ns	30.0 \pm 1.4, 58	36.3 \pm 1.1, 10	34.8 \pm 1.1, 25	36.3 \pm 0.6, 3	25.9/30.5 ⁵	28.3 \pm 1.3, 6
Tarsus min. w	3.3 \pm 0.3, 31 ***	3.1 \pm 0.2, 50	3.6 \pm 0.3, 10	3.5 \pm 0.4, 22	3.3 \pm 0.4, 3	2.7	3.4 \pm 0.1, 6
Tarsus distal w	10.0 \pm 0.4, 32 ns	6.8 \pm 0.5, 51	7.7 \pm 0.5, 10	7.1 \pm 0.4, 22	7.0 \pm 0.4, 3	6.5	7.4 \pm 0.2, 6
Middle claw l	10.7 \pm 0.6, 32 ***	9.9 \pm 0.7, 53	11.8 \pm 0.6, 9	10.7 \pm 0.6, 22	11.2 \pm 0.4, 3	9.7	10.6 \pm 0.5, 6
Middle claw d	2.3 \pm 0.2, 32 ***	2.1 \pm 0.2, 54	2.4 \pm 0.2, 9	2.4 \pm 0.2, 22	2.1 \pm 0.1, 3	2.0	2.1 \pm 0.1, 6
Hind claw l	8.8 \pm 0.6, 25 ***	8.2 \pm 0.6, 45	9.0 \pm 0.7, 9	8.8 \pm 0.4, 16	8.3 \pm 0.6, 3	8.2	8.9 \pm 0.4, 6
Rictal bristle l	25.3 \pm 2.5, 33 ***	28.2 \pm 2.7, 55	23.0 \pm 1.7, 10	25.3 \pm 1.9, 23	25.5 \pm 0.7, 3	25.6	21.8 \pm 0.9, 6
Auricular l	18.0 \pm 2.4, 43 ***	22.5 \pm 2.7, 80	14.4 \pm 1.9, 10	18.0 \pm 1.8, 22	15.4 \pm 0.8, 3	20.5	14.4 \pm 0.6, 6
Tarsal feathering, front ¹	4.6 \pm 1.7, 32 ***	6.9 \pm 1.5, 58	9.3 \pm 1.8, 10	15.6 \pm 2.4, 24	13.0 \pm 4.6, 3	13.6	4.1 \pm 0.8, 6
Tarsal feathering, rear ²	7.1 \pm 4.9, 32 ***	17.49 \pm 7.9, 57	7.2 \pm 1.8, 10	9.5 \pm 1.3, 23	9.5 \pm 2.6, 3	8.3	0 \pm 0, 6
Percent of tarsus feathered ³	80.8 \pm 9.9, 31 ***	59.5 \pm 14.1, 57	77.3 \pm 4.4, 10	64.0 \pm 4.3, 22	68.9 \pm 4.6, 3	57.7	92.7 \pm 1.3, 6
Pale tail band w ⁴	3.0 \pm 0.6, 31 ns	3.1 \pm 0.7, 55	2.7 \pm 0.5, 10	2.2 \pm 0.4, 11	1.9 \pm 0.4, 3	1.4	2.1 \pm 0.3, 6
Dark tail band w ⁴	7.7 \pm 1.3, 31 ***	6.7 \pm 1.2, 55	6.5 \pm 1.4, 10	6.4 \pm 1.4, 12	6.7 \pm 0.7, 3	3.3	4.9 \pm 0.9, 6
Wing-tail ratio	1.8 \pm 0.1, 30 ***	2.0 \pm 0.1, 53	2.0 \pm 0.1, 9	2.0 \pm 0.5, 19	2.0 \pm 0.1, 3	2.0	2.0 \pm 0.1, 6

¹From distal edge of feathering to centre of first joint on middle toe. ²From proximal edge of hallux. ³Feathered length averaged over both sides; see Methods

⁴Approximate measure at middle of central rectrix. ⁵Second set of measurements from Herremans et al 1999

prominent streaking on the mantle, and finer barring and vermiculation of the underparts.

At any single locality from which several specimens originate, the intralocality variation is roughly equivalent to the variation in that species, judging by Factor 1 scores. For *uadagascariensis* at Tabiky, Factor 1 scores range from *c.* 0 to 2.5 ($n = 13$), and at Namoroka, from *c.* 0.5 to 2.2 ($n = 3$), while for *rutilus*, scores from both Andapa ($n = 8$) and Sianaka ($n = 28$) range from -1.0 to 0. As none of these sites seem to be likely zones of overlap, these levels of variability appear independent of possible intergradation, and they indicate that the observed variation is not clinal in nature. In a PCA between *rutilus* and *uadagascariensis* using eight morphological variables, loadings for auricular extension length, rictal bristle length, and extent of unfeathered anterior tarsus were strongly positive on Factor 1, while the loading for tail length in particular was strongly negative on Factor 1 (Table 2). There was virtually no overlap between the mostly negative Factor 1 scores of *rutilus* and the mostly positive scores of *uadagascariensis*; mean factor 1 scores were highly significantly different between the species (Table 2). Factor 1 is a shape axis showing that birds with long auricular and rictal bristles and more extensively naked front tarsi also had short tails (*rutilus*), while birds with short bristles and more feathered tarsi had long tails (*uadagascariensis*). Factor 2, although with a significant eigenvalue, did not differ between the two groups in any discernible pattern, nor in mean group factor scores. In a DFA using the same variables, specimens of *uadagascariensis* were 100% correctly classified, while 89% of *rutilus* specimens were correctly classified (Table 2). The approximate F values were highly significantly different ($P < 0.0001$) between *uadagascariensis* (Approximate $F = -2.35 \pm 0.62$, $n = 20$) and *rutilus* (Approximate $F = 1.07 \pm 1.13$, $n = 44$; Table 2). Of the plumage characters that were scored for adults, all were highly significantly different between *uadagascariensis* and *rutilus* (Table 3).

Vocalizations

The number of phrases in the songs of both taxa varies from 3 to 11; this variation has no geographic component. In most other characters measured, however, there are significant differences between the songs of *uadagascariensis* and *rutilus* (Table 4). The song of *rutilus* is typically very simple: a series of phrases of *c.* 0.16 s, each phrase separated by an interval of *c.* 0.21 s, and from *c.* 0.65 to 1.04 kHz in frequency (Fig. 3). Each phrase almost always consists of a single, clear note with a flat shape (i. e., all on one frequency). It is apparent from the waveform display (as shown by Canary), however, that in the songs of some individuals of *rutilus* the phrases may be slightly 'pulsed' (to a level audible to the human ear), although in almost all such cases the phrase is clearly represented as a single note on the accompanying sonagram (e.g., Fig. 3, song from Périnet). Very rarely, however, a single phrase in a *rutilus* song may contain two separate notes (e.g., the first phrase of songs of LNS 95695, recorded at Ranomafana). Harmonics in the song are rare, and when present are

TABLE 2.

Component loadings and summary statistics for principal components analysis (PCAs of Factors 1-3 and discriminant functions analysis (DFA) for *Otus rutilus* and *O. madagascariensis* (combined in the PCA and DFA but grouped separately for two-sample *t*-tests with separate variances).

Abbreviations as for Table 1.

Variable	PCA Component	DFA Classification			
	loadings	functions	<i>madagascariensis</i>	<i>rutilus</i>	F-to- remove
	1	2			
Eartuft 1	0.48	0.56	-1.16	-1.09	0.09
Auricular extension 1	0.83	0.15	2.94	3.42	4.10
Rictal bristle 1	0.70	0.35	1.69	2.03	2.23
Wing 1	-0.20	0.74	5.28	5.40	1.04
Primary 1 1	-0.43	0.64	0.57	0.48	0.46
Tail 1	-0.75	0.39	4.91	4.26	13.34
Tarsus 1	-0.28	-0.07	16.79	16.83	0.01
L of bare tarsal in front	0.77	0.08	3.45	4.72	10.13
Eigenvalues	2.86	1.58	—	—	—
Constant	—	—	-934.59	-922.98	—
% variance explained	35.73	19.78	—	—	—
$\bar{x} \pm \text{s.d.}, n$ (<i>madagascariensis</i>)	1.15±0.52, 21	-0.01±0.96, 21	—	—	—
$\bar{x} \pm \text{s.d.}, n$ (<i>rutilus</i>)	-0.52±0.64, 44	-0.01±1.04, 44	—	—	—
<i>t</i> , <i>df</i> , <i>P</i>	11.28, 47.6, 0.000	-0.07, 42.3, 0.943	—	—	—

TABLE 3.

Summary statistics (mean ± s.d., n) and significance tests (Kruskal-Wallis one-way analysis of variance) for qualitative morphological characters mapped in Fig. 1 for adults of *Otus rutilus* and *O. madagascariensis*. Significance levels as in Table 1.

Variable	<i>madagascariensis</i>	<i>rutilus</i>	Mann-Whitney <i>U</i>
Overall colour (1 = rufous, 4 = grey)	2.68±0.67, 33	1.86±0.66, 57	1505.0***
Rim of facial disk (1 = obsolete, 4 = prominent)	3.75±0.42, 32	1.92±0.65, 54	1700.0***
Back streaking (1 = obsolete, 4 = prominent)	3.61±0.57, 33	1.97±0.72, 56	1750.5***
Coarseness of underparts (1 = coarse, 4 = fine)	3.71±0.37, 35	2.44±0.90, 57	1767.5***
Tail banding (1 = vague, 4 = prominent)	3.65±0.49, 33	2.48±0.80, 55	1579.0***

TABLE 4.

Summary statistics (mean \pm s.d., n) for measurements of vocal parameters of *Otus madagascariensis* and *O. rutilus*. $F_{\min 1}$ was minimum frequency of lower band, $F_{\max 1}$ maximum frequency of lower band; $F_{\min 2}$ and $F_{\max 2}$ were the same measures for the higher band; Total F_{\min} and F_{\max} were the lowest and highest frequencies, whether the bands were measured separately or not. Analyses were done on means from each tape cut (numbers of individuals taped per site and phrases per individual are given in Appendix 2), which were tested using two-sample t -tests with separate variances: significance levels as for Table 1.

	Taxon		t	Component loadings	
	<i>madagascariensis</i>	<i>rutilus</i>		Factor 1	Factor 2
Number of phrases	6.60 \pm 1.79, 20	6.01 \pm 1.69, 16	0.92 ns	0.35	0.90
Number of notes phrase	1.78 \pm 0.68, 12	1.02 \pm 0.06, 12	3.88 **	—	—
$F_{\min 1}$	0.34 \pm 0.12, 12	—, 12	—	—	—
$F_{\max 1}$	0.65 \pm 0.21, 12	—, 12	—	—	—
$F_{\min 2}$	0.85 \pm 0.09, 12	0.65 \pm 0.05, 12	7.05***	—	—
$F_{\max 2}$	1.32 \pm 0.06, 12	1.11 \pm 0.08, 12	7.21***	—	—
Total F_{\min}	0.49 \pm 0.17, 20	0.66 \pm 0.06, 16	4.01***	0.87	-0.12
Total F_{\max}	1.23 \pm 0.16, 20	1.02 \pm 0.18, 16	3.56***	-0.83	0.33
Frequency range	0.73 \pm 0.30, 20	0.36 \pm 0.21, 16	4.45***	—	—
Phrase length	0.13 \pm 0.03, 20	0.15 \pm 0.06, 16	1.01 ns	—	—
Interval length	0.30 \pm 0.07, 20	0.21 \pm 0.03, 16	5.26***	-0.40	-0.16
PCA					
eigenvalues	—	—	—	1.75	0.96
% variance explained	—	—	—	43.65	24.02
Mean loadings Factor 1	-0.56 \pm 0.89, 20	0.70 \pm 0.63, 16	4.84***	—	—
Mean loadings Factor 2	0.25 \pm 0.97, 20	-0.31 \pm 0.97, 16	1.74 ns	—	—

displayed much more faintly on the sonogram than are the primary bands, and appear at $c.$ 1.45 to 1.75 kHz.

The song of *madagascariensis* differs from that of *rutilus* in several important respects. The harmonic structure is very strong in *madagascariensis*, and is characterized by two strong bands on the sonogram (Fig. 3). The frequency range is $c.$ 0.34 to 0.65 kHz for the lower tone, and $c.$ 0.85 to 1.32 kHz for the higher tone. This gives the song of *madagascariensis* a greater overall frequency range, but also causes it to sound lower and 'gruffer' to the human ear than in songs of *rutilus*. Furthermore, each phrase of the song of *madagascariensis* consists typically of two, three or more very short notes (homologous to the single-note phrases of *rutilus*), contributing to a noticeable 'warbling' quality to the song. Frequently, each short note of *madagascariensis* is also sharply inflected, resembling an inverted 'V', in contrast to the flat shape of the notes in *rutilus* (Fig. 3). Compared with songs of *rutilus*, the phrases are slightly but significantly shorter in *madagascariensis*, while the inter-phrase interval is slightly but significantly longer (Table 4).

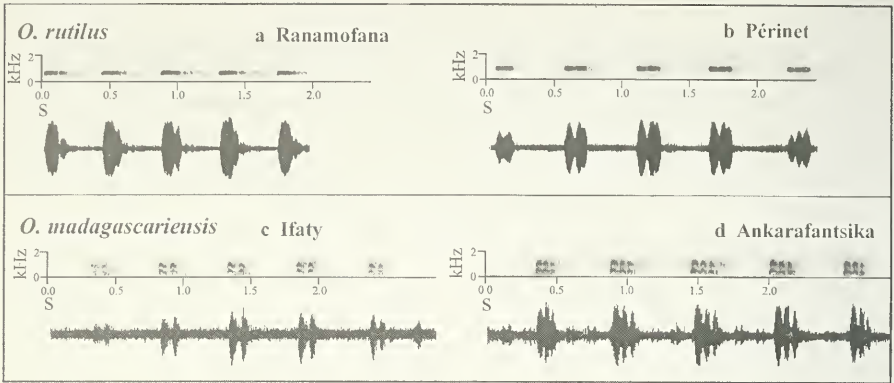


Fig. 3. Sonograms and waveform displays for songs of *Otus rutilus* (a, b) and *O. madagascariensis* (c, d). a) Typical song of *rutilus*: a short series of phrases, each of which consists of only a single flat note (rarely two notes per phrase) without or with very weak harmonics. Recorded at Ranomafana by TSS (LNS 95695). b) Rare variant song of *rutilus*: each phrase consists of a single note, but the waveform display indicates two separate pulses of sound per note, creating a slight audible warbling effect. Recorded without tape playback at Périnet by J. E. Pierson (JEP 091208a). c, d) Typical songs of *madagascariensis*: a short series of phrases, each phrase containing two to four very short inflected notes, each with strong harmonics. Recorded in response to tape playback by TSS, for c) at Ifaty (LNS 87973), and for d) at the Réserve Naturelle Intégrale d'Ankarafantsika (LNS 95648).

Recordings from across large areas of Madagascar (Appendix 2, Fig. 3) show little variation within either of the two vocal types, and little or no evidence of intergradation in vocal characters. In southeastern Madagascar, a relatively well-sampled region, our quantitative analysis reinforces the qualitative impressions discussed by Goodman *et al.* (1997) of an abrupt transition in song type in Malagasy *Otus* across a very steep environmental gradient. However, there are a few exceptions to this generally low level of variability, as follows. Of the several *O. rutilus* (*s.l.*) sound recordings archived at NSA as of 1998, only one did not fit the normal pattern described above: in a recording from Berenty (NSA 35229), one singing bird is an obvious *madagascariensis* while another in the background resembles *rutilus*. Whether the latter was a true *rutilus*, a variant song of *madagascariensis*, or evidence of intergradation is unknown, and the quality of this Berenty recording is too poor to provide quantitative data. We have very few recordings of *Otus* from the High Plateau of central Madagascar; a single recording from Ihosy retains very strong harmonic structure, typical of *madagascariensis*, but the phrases in this song are also comprised of only a single note, typical of *rutilus*. With such a small sample, it is unclear whether this song type represents a pattern in variation across the High Plateau. Songs at Antananarivo and from near Lake Itasy, however, sound to the ear like typical *madagascariensis* (AFAH, pers. obs.). Another region where *madagascariensis* and *rutilus* probably come into contact is in the northwest, where the humid forest of the

Sambirano district is bordered by deciduous forest (albeit of different types) both to the north and south. Our only tape-recorded song from this region, from the island of Nosy Be, has characteristics of both taxa (Fig. 4) but sounds like *madagascariensis*, and several other individuals heard on Nosy Be in secondary habitats also all sounded like typical *madagascariensis* (AFAH, pers. obs.), although the single adult specimen (MNHN 1866-148) from there, collected by Grandidier in 1866, is *O. rutilus*. It is still unclear whether both species occur at Nosy Be, or if *rutilus* has been displaced to some extent by *madagascariensis*, as the rainforest habitat of the former has now been mostly destroyed.

Despite the striking vocal differences between *madagascariensis* and *rutilus*, they escaped notice until C. W. Benson and G. S. Keith called them to J. T. Marshall's attention. Marshall (1978: 19) briefly noted (but did not describe) a geographical component to the distribution of the song types of *Otus rutilus* (*s.l.*), and reported that Keith heard one bird that 'switched from one song to the other.' As discussed elsewhere (Goodman *et al.* 1997: 52), Keith actually heard 'both song types from the same patch of forest' at Fanpanombo, near Maroantsetra, northeastern Madagascar, but stated 'We did not see the birds (they were on the other side of a river). So whether these are simply alternative calls made by the same individual, or male-female calls, or what, I don't know' (Keith *in litt.* to TSS, 22 March 1990). The area near Maroantsetra, in the heart of the eastern rainforest, would seem to be an unlikely location in which to find *madagascariensis* or a bird with an intermediate song, and our two recordings from near here, on the Masoala Peninsula, are typical of *rutilus*. However, Maroantsetra is not far north of Ambatovaky, from whence comes another seemingly anomalous record of a 'quintessentially western' species, the White-breasted Mesite *Mesitornis variegata* (Thompson & Evans 1992). In any event, there are no tape recordings of the bird (or birds) heard by Keith at Maroantsetra. Perhaps what Keith heard was a normal *rutilus* and an individual of *rutilus* exhibiting the slightly 'pulsed' effect described earlier.

Type specimens

Otus rutilus

The original description of *rutilus* is a footnote by Pucheran (1849a), who described it as being rather bright russet-red above with black streaks and transverse fawn spots, and having a longitudinal white band across the scapulars, short ear tufts concolorous with the upperparts, and the underparts much paler, each feather with small white bars. He did not say from how many specimens the description was drawn, and the locality was given only as 'Madagascar'. However, Pucheran (1849b) gave a full description of one of Bernier's specimens (now MNHN 1999-892; all MNHN specimen numbers cited herein refer to the 'Catalogue général'), and it was figured in colour (Pucheran 1849b). This specimen also has the annotations on its stand '*Scops menadensis* [a variant spelling of *manadensis*] Q et G.; *Scops rutilus* Puch.; Type; fig. dans les vélins' [figured on a calf skin, J.-F. Voisin, *in litt.*]. The other rufous Bernier specimen (MNHN 1834-90) is now also labelled as a type, but



Fig. 4. Scores for quantitative vocal characters of *Otus rutilus* and *O. madagascariensis* mapped against vegetation zones (as in Fig. 1). In order, from left to right, characters are: number of notes (white < 1.0, black > 2.0); internote interval (white < 0.2, black > 0.3); minimum frequency or total F_{\min} (white > 0.6, black < 0.4); maximum frequency or total F_{\max} (white < 1.0, black > 1.2). Number to left of bar is site number (details in Appendix 2); number to right is n for locality.

it is more saturated rufous and less marked overall (and thus does not match the original description well), as noted by Pucheran (1849b), and on its stand are the words 'Type' and '*menadensis*' (but not '*rutilus*'). Both the Bernier specimens listed above are rufous, and clearly belong to the eastern species. However, because the provenance of both specimens is unknown and could differ, we designate MNHN 1999-892, the bird referred to in Pucheran's (1849a) description, as the lectotype of *Otus rutilus*. Bernier collected in the east and the north-east (Rand 1936), to which general region we restrict the type locality.

Gray (1869) cited the date of Pucheran's (1849b) fuller description and plate as 1844 which, if correct, would have year priority over the footnote that is considered the original description (Pucheran 1849a). However, the date attributed by Gray is almost certainly due to the fact that Vol. 4 of the journal in which Pucheran (1849b) appeared has an 1844 date on the title page, a date which can hardly apply to the later numbers of Vol. 4, as Pucheran (1849a) is referred to in Pucheran (1849b). Vol. 3 is dated 1843, but Vol. 5 is undated, and vol. 6 is dated 1852 (F. E. Warr, *in litt.*), so the appearance of this journal was clearly irregular. In most synonymies, Pucheran (1849b) is simply listed without a date but following Pucheran (1849a), and its true date may be post-1849.

Although Kaup (1852: 229) placed both of Bernier's rufous specimens under *rutilus*, he listed a brown specimen (MNHN 1999.891), also collected by Bernier (but unaccountably not mentioned by Pucheran 1849b) under *manadensis*, although he doubted its Madagascar provenance. This was the original basis for the listing of *manadensis* from Madagascar (and for the consequent lumping of these species); nevertheless, Bernier's brown specimen is clearly a brown morph *rutilus* (with, among other features distinguishing it from *manadensis*, long rictal bristles and larger overall size).

Otus madagascariensis

The only name in synonymy under *Otus rutilus* that could potentially represent the western Malagasy population is *Scops madagascariensis* Grandidier 1867. This species was described (Grandidier 1867a: 85-86) as smaller and distinctly darker than the Tropical Screech-Owl *Otus choliba* (= *brasiliensis*). Grandidier's 1866 expedition took him along the west coast of Madagascar, and in Grandidier (1867a) he stated that the first 12 bird species he described therein (of which *Scops madagascariensis* was the second) were from the southwest coast of Madagascar.

However, no recognized type specimen of *Scops madagascariensis* is present in MNHN, where many (if not all) of Grandidier's bird types are deposited (as well as many of his mammal types, C. & J.-F. Voisin, *in litt.*). Furthermore, Grandidier (1867a) did not indicate upon how many specimens the description was based. There are two mounted scops-owls at MNHN collected by Grandidier, one of which (MNHN 1866-148), a rufous bird collected at Nosy Be, is ruled out as Grandidier's type both on plumage and distribution. The other Paris Grandidier specimen (MNHN 1867-774), a female from the southwest coast, is fairly dark brown, as required by Grandidier's

(1867a) brief description. A third Grandidier specimen (USNM 352819, originally MNHN 1867-773), also from the southwest coast and dated 1867, was exchanged to the USNM in 1886 (J.-F. Voisin, *in litt.*). The original number of the USNM specimen is consecutive with that of MNHN 1867-774 and apparently came from the same voyage. Nevertheless, it is not listed as a type in the USNM specimen catalog or by Deignan (1961), nor is this designation present on its label, and its pale brown colour does not match Grandidier's description of *madagascariensis*. However, MNHN 1867-774, a typical adult of the southwestern population, is compatible with the description. Although it is labelled only *Scops menadensis*, rather than as a type or as *Scops madagascariensis*, this must be due to the fact that the species' describer had already synonymized it prior to the specimen's arrival in Paris and its being mounted on the stand that bears the data and name. The status at the MNHN of Grandidier's types of *Coua* species (Voisin & Voisin 1999) is consistent with this interpretation: the types of his three valid species of *Coua* have the word 'Type' written on the label and/or stand, while the type of his *C. pyropyga*, long in synonymy, lacks the type designation on its label and stand. We therefore designate MNHN 1867-774 as the name-bearing lectotype of *Otus madagascariensis* (Grandidier 1867).

'Torotoroka' is an onomatopoeic Malagasy name for scops-owl, which, although until now perhaps not strictly applied to western birds, does recall the two-noted, structured song of *madagascariensis* rather than the simple one of *rutilus*. Each 'o' in Torotoroka is pronounced as 'oo', and the 'a' is de-emphasized. We propose 'Torotoroka Scops-Owl' as an appropriate common name for *Otus madagascariensis*. Because of the long-term use of other common names to refer to both taxa, a new English name for *Otus rutilus* is also desirable. We suggest 'Rainforest Scops-Owl' for *rutilus*, which so far as known is confined to this habitat, where it is the island's only scops-owl.

Discussion

Although Grandidier (1867a) correctly named the scops-owl from the southwestern coast of Madagascar as a new species, he did so naively, as he was in Madagascar with few comparative resources, and he did not even mention *rutilus* in his description. Within a few months he became convinced that *madagascariensis* was the brown morph of *Otus manadensis* (Grandidier 1867c).

The earliest series of *rutilus* (*s.l.*) was that collected by Pollen and van Dam for the Museum Pays-Bas (now NNM) between 1865 and 1871. Regional differences in this series were not noted in reviews of the collection (Schlegel & Pollen 1868, Schlegel 1873, Finsch 1898). Specimens of *rutilus* from Pasandava Bay in this series look fairly similar to the Morondava specimens of *madagascariensis*, so the differences would have been easily overlooked, especially since Schlegel (1873) placed them all in *manadensis*. The most obviously different specimen in this collection, a rufous morph *rutilus* collected by Audebert (NNM Cat. No. 14) in an unspecified eastern locality, was acquired only after Schlegel's works.

Sharpe (1875a), despite his detailed descriptions of rufous and brown morph *rutilus*, nevertheless stated that the differences among BMNH specimens were not very considerable. Only seven skins of *rutilus* were then held in the collection, none with specific localities; six of these were collected by Crossley, the other by Pollen in NE Madagascar (Sharpe 1975a). Of the Crossley skins, one is a downy juvenile labelled 'SE', the others adults, one labelled simply 'Madagascar', one 'N', one 'SE', and two (those described by Sharpe 1875a, now BMNH 1875.2.1.9 and 10) as 'SW' Madagascar. The last two, however, are both dark and richly coloured and do not differ from the other *rutilus* for which region of origin is specified in any salient features, and they show all the characters of *rutilus* rather than of *madagascariensis*. The annotation 'SW' was written in a different hand, above the word 'Madagascar', and in a lighter ink, while the designations 'SE' and 'N' must have been written on the labels at the same time as was the word 'Madagascar', as they seem to be in the same hand and ink, and on the same line as 'Madagascar'. The register lacks the designation 'SW' for BMNH 1875.2.1.9 and 10, and as the data would have been entered therein from the labels, the regional annotation was probably added to the labels later that year, since they were published by Sharpe (1875a) as being from the 'SW'. Sharpe's (1870, 1871, 1872, 1875b) relevant papers do not place Crossley in western Madagascar, nor do they include species restricted to the west. Although Sharpe (1875b) noted that when last heard of Crossley was heading toward the west coast, whether he arrived is uncertain (P. Jenkins, *in litt.*), and no letter detailing Crossley's whereabouts accompanied the last shipment (Sharpe 1875b). Since Crossley died in 1870 and his collections were dispersed through dealers (Mittermeier *et al.* 1994), a mix-up with his localities seems highly likely. Scops-owls definitely from southwestern Madagascar do not approach the two Crossley 'SW' birds in morphology, and these two individuals also group with statistical confidence among eastern birds. Thus, Sharpe (1875a) had no true *madagascariensis* available to him for study, and his conclusion of limited variability was based on specimens with apparently incorrect regional designations, which may have misled subsequent researchers as well.

The Archbold-Vernay Expedition (FAA, Mission Zoologique Franco-Anglo-Américaine à Madagascar) resulted in at least 42 new specimens of *rutilus* (*s.l.*) between 1929-1931, which were divided mainly among the BMNH, MNHN, and AMNH. Nine of the 15 FAA specimens that went to BMNH (but none of those that went to other museums) were originally labelled '*Otus scops pallidior*', and were entered as such into the register (F. Steinheimer, *in litt.*). Those labelled as *pallidior* were collected during each of the three years of the expedition, but most of them were pale, finely marked birds from drier western localities, while two *rutilus* were also labelled '*pallidior*'; one of these is a *madagascariensis*-like immature from near Maromandia (BMNH 1931.8.18.362) and, the other, unaccountably, is a typically coarsely marked dark adult from near Anaborano (BMNH 1931.8.18.363). The FAA specimens in the BMNH that are not so marked are all from eastern rainforest localities, and are clearly *rutilus* in morphology. The name '*pallidior*' was apparently

written by W. H. Perrett, a clerical officer (F. E. Warr *in litt.*). It is unclear by whom or on what basis the identifications were made, and this name was not mentioned by Rand (1936) in his treatment of the FAA expedition. On the labels, '*pallidior*' later was crossed out and replaced by '*rutilus*'. It seems that the name '*pallidior*' was never previously published, so it has no taxonomic standing (and its mention herein is intended only as relevant background information, not as formal publication), but its existence on these labels suggests that an unidentified individual who was studying the BMNH series sometime between 1931 and 1936 had recognised differences between eastern and western birds.

There is yet another indication that the morphological variation within *rutilus* (*s.l.*) had previously been perceived as excessive for a single species. Of the three specimens at the ROM, one (ROM 41717) is a typical, richly coloured *rutilus* from Rogez in 1922, while the other two, which were collected in the 1960s from the southwest coast, exhibit classic *madagascariensis* morphology, and differ strikingly from the eastern bird. Both of the south-western specimens (ROM 99472 and 99473) were initially identified as '*Otus* ?n. sp.', but this was then crossed out and replaced with '*Otus r. rutilus*'.

Distribution, habitat and status

Otus rutilus is found, so far as known, only in areas of eastern rainforest habitat (Hawkins 1999), from sea-level to 2,050 m (Figs. 1, 2, 4; ZICOMA 1999). It may be very common, with up to five singing birds audible from one spot (AFAH, pers. obs.), but the degree to which it can withstand habitat alteration is unclear. *Otus madagascariensis*, however, appears to be more adaptable and widespread, being found not only in drier western forests (Figs. 1, 2, 4), but also in trees in villages and other degraded habitats, even on the central plateau. However, there are few records from this region (Dee 1986) and only one such specimen has been examined for this study, from Ivohibe, along the western edge of the rainforest belt. Although its upper altitudinal limits remain to be determined, *O. madagascariensis* is not known from higher elevations. Further field and museum work is needed to establish the full distributions of these taxa and to determine how they behave in zones of potential contact, as well as how they respond to habitat changes.

Other western Indian Ocean island taxa

Because all the following scops-owl taxa have been considered conspecific with *Otus rutilus* (*s.l.*), and because the Mayotte taxon still is, we reconsider the status of all of these taxa based on study of specimens; sonagrams have already been published elsewhere for most of these taxa. All the Comoran taxa differ from both *madagascariensis* and *rutilus* in having the ear tufts not much longer than the surrounding feathers, and in lacking a prominent white supercilium. They differ from *rutilus* in having most of the rear tarsus feathered (Table 1), in their relatively longer

tails, and in having reduced rectal bristles and distal extensions of the auriculars. Compared with *madagascariensis*, they have higher wing/tail ratios, less extensively feathered tarsi, narrower dark tail bands, and less graduated tails. All Comoran taxa (except *panliani*) have much larger bills, longer wings, and longer tarsi compared with both *madagascariensis* and *rutilus*. All (except *mayottensis*) have relatively small claws, less extensive feathering on the anterior distal tarsi, reduced or missing white scapular spots, and more narrowly banded tails than in the Malagasy taxa.

Otus mayottensis

Adult Mayotte Scops-Owls *Otus* [*r.*] *mayottensis* resemble some *rutilus*, but their contour feathers are stiffer and not as soft, and the tarsi are more fully feathered along the posterior side than in *rutilus*. Compared to both *rutilus* and *madagascariensis*, *mayottensis* is much larger (Table 1); its throat is more prominently streaked and barred; the background colour of the underparts is darker, with few and irregular pale markings and reduced white patches; and the tarsal feathering is darker. Compared to *madagascariensis*, *mayottensis* has a reduced dark rim to the facial disk; a much darker background colour overall; less prominent streaking on the mantle; and a relatively short and less strongly banded tail. Two previously mentioned distinctions between *mayottensis* and *rutilus* (*s.l.*), the apparent presence of more white around the face and a more prominent buffy collar in *mayottensis* (Benson 1960), are largely due to differences in preparation style. A third perceived difference mentioned by Benson (1960), the less bold black streaking below in *mayottensis*, is due to the darker ground colour of its underparts. The song of *mayottensis* is most similar to the two Madagascar species, but is lower and deeper, with longer notes that lack internal structuring and harmonics (Lewis 1998; NSA 51549). Thus, although *mayottensis* is clearly closely related to *rutilus* and *madagascariensis*, all three are probably better treated as full species, and we suggest for the former the common name of Mayotte Scops-Owl, essentially as already used by Lewis (1998). *Otus mayottensis* exists down to sea level in disturbed woodland and mangroves (Louette 1988, Hornbuckle 1997).

Two scops-owls from Mayotte in Paris are labelled as types of '*Scops humbloti*' Oustalet. However, Benson (1960) was unable (as were we) to locate any published use of this name and, since '*humbloti*' was neither used by Milne-Edwards & Oustalet (1888) nor listed in their synonymy, Benson (1960) described *mayottensis* as new. Benson (1960) could locate only one (MNHN 1884-2065) of the two specimens registered into the Paris collection as '*humbloti*', but the second specimen (MNHN 1884-2066) was found by PCR in the MNHN mounted collection. It is labelled '*Scops Humbloti* Oust., Humblot, Mayotte', with only the 'T' of what was evidently the word 'Type' still legible. This immature *mayottensis* has finely patterned underparts and prominently banded tertials and tail, and thus (as with immature *rutilus*) resembles *madagascariensis* more than do adults of *mayottensis*.

Otus capnodes

The Anjouan Scops-Owl *Otus capnodes* differs from *rutilus*, *madagascariensis*, and *mayottensis* in having very soft, usually darker, plumage with less streaking and more prominent, more even barring overall; longer fluffier crown feathers, nearly eclipsing the ear tufts; the facial disk either plain whitish, whitish with fine concentric dark rings, or (in blackish individuals) all-dark, with a prominent blackish outer rim; the auricular extensions sparse and short; very narrow banding on its rather long, square tail; and long tarsi (Table 1) that are much less extensively feathered along the front, but much more heavily and fully feathered along the rear; relatively small claws; and a mostly pale horn bill with darker cutting edges. In addition, in those *capnodes* that have scapular spots, these are inconspicuous, buffy, and narrowly barred dark. The immature plumage of *capnodes* is more similar to adult plumage than in the foregoing species. *Otus capnodes* is morphologically much more distinct from *mayottensis*, *madagascariensis*, and *rutilus* than any of these are from each other. Its song is also very different, being a whistle quite unlike the songs of other scops-owls (Safford 1993).

Despite Gurney's (1889) good description of *capnodes*, Finsch (1898) considered it identical to *rutilus*, an ill-considered decision (very likely due to Finsch's self-acknowledged lack of *capnodes* specimens) that nevertheless has influenced taxonomy to the present. Many of the Leiden scops-owl mounts have lost some of their tarsal feathering, probably due to preparation techniques. This, and the existence of a very dark specimen of *madagascariensis* at NNM, may have led Finsch (1898) to discount the specific value of the different leg feathering and dark colouration that Gurney (1889) had noted. Perhaps adding to the confusion, in the Rothschild Collection (now at AMNH) there were three *capnodes* labelled as being from Madagascar, and while they were correctly identified to taxon the regional designation had not been marked as questionable.

At least 47 specimens of *Otus capnodes* exist (AMNH 8 [not 4 as stated by Benson 1960], ZMUC 2, BMNH 12, USNM 3, SMF 1, ROM 2, MCZ 1, MNHN 17, LIVCM 1 [see *O. pauliani*]), and the absence of strongly rufous birds among this sample suggests that such a morph either does not exist or is very rare. However, a blackish-brown morph seems common, being represented by about 12 specimens.

The selected syntype of *capnodes* (BMNH 1955.6.N.20.3848) was said to be 'Coll. by G. A. Frank' (Warren 1966: 51). However, *capnodes* was probably collected only by Humblot (Benson 1960), and the unmounted specimens all resemble each other in preparation. As independently noted by Benson (1999), G. A. Frank, Jr. was a dealer who bought up many of Humblot's Comoro duplicates (Sharpe 1906: 354), and the selected type is a remade mount from the Norwich Museum. Incidentally, there are two other syntypes at BMNH, and the Cambridge collection also holds two syntypes of *capnodes*, which have their labels annotated 'Humblot through Franck [*sic*], 1888'. Also, the listing of the type locality of *capnodes* as 'from forest of E. Imerina; Anjouan' (Knox & Walters 1994: 170) erroneously incorporates a Madagascar locality, and should read simply 'Anjouan'.

Otus moheliensis

The recently described Moheli Scops-Owl *Otus moheliensis* (Lafontaine & Moolaert 1998) seems morphologically intermediate between *capnodes* and *mayottensis*. It is similar in size to *capnodes*, but differs from it having a bright rufous morph; stiffer, more compact plumage; short eartufts and crown feathers; more streaking and little or no barring above; nearly unicoloured underparts with greatly reduced pale bands; much shorter and less dense feathering on the rear tarsus; and an all-dark upper mandible. *Otus moheliensis* is larger (Table 1) than either Madagascar species but smaller than *mayottensis*, and differs from all three in having short eartufts; reduced rectal bristles and distal extensions to the auriculars; little streaking below; small, barred scapular spots; paler tertials; and less extensively feathered tarsi. Compared only to *mayottensis*, *moheliensis* has a much more prominent black rim to the facial disk; warmer, more saturated overall colour in the brown morph; paler background colour above and more prominent overlying dark markings; and weaker claws and feet. The typical song of *moheliensis* is evidently a sequence of hisses, and it also gives a screech call much like that of *capnodes* (Lafontaine & Moolaert 1998).

Otus pauliani

The Grand Comoro Scops-Owl *Otus pauliani* is much the smallest of the group, with a very small bill and short wings (Table 1). It resembles *capnodes*, with soft and lax plumage, no prominent eartufts but long crown feathers, and full, fluffy feathering on the rear edge of the proximal half of the tarsus. However, compared to *capnodes*, its head is much more barred and greyish; its rectal bristles are profuse but fairly short, its facial disk is rudimentary with very decomposed and fluffy auricular feathers, and lacks a dark rim: the body is finely and evenly barred with blackish on a buffy-ochre background, with some whitish barring below; the tarsal feathering is barred dark: the bill is dark with a pale tip and gonys ridge in the skin; and the claws are about half dark. Five individuals seen and/or photographed had dark eyes (Herremans *et al.* 1991), while the iris colour of the type specimen was recorded as being yellow, and one photographed had yellowish eyes (Lewis 1996).

Only a single specimen of this species was ever collected, and it is an immature, but a living individual photographed by Lewis (1996) closely resembles this specimen. The song of *pauliani*, which is a very long series of 'chaw' notes repeated at about 2/sec, is highly distinct from those of any of the other taxa (Benson 1960, Herremans *et al.* 1991, König *et al.* 1999), and hence this bird must be treated as a distinct species. It was originally treated as a subspecies of *rutilus* only in deference to the opinions of others (Benson 1960: 61). Its upper montane (c. 1,000-1,850 m) forest-heathland habitat is also unusual for the group; although *rutilus* has now been found up to 2,100 m (ZICOMA 1999), at higher elevations it occurs in montane forest, not heathland.

An *Otus* specimen (LIVCM T13096) was labelled and published as having been collected on Grand Comoro by Humblot in 1886 (Tristram 1889). PCR compared the 'Grand Comoro' bird directly with the entire BMNH holdings of *capnodes*

(including the unique type of *pauliani*), and in all respects it is clearly *capnodes*. It appears typical in external preparation style to Humblot's large Anjouan series. In addition to re-copied museum labels, the 'Grand Comoro' specimen bears what appears to be an original label, but the handwriting and content thereon does not closely match that of Anjouan *capnodes* specimens at BMNH, for which the 'original' labels vary depending on the dealer (Frank or Boucard) from whom they were obtained. At MNHN, the official 'C.G.' labels are the only labels on 11 *capnodes* specimens, with the writing and content different yet again. This suggests that Humblot's specimens may not have been labelled until after their dispersion and, if so, a mistaken attribution of this specimen to Grand Comoro, on which Humblot collected during the same time period (Benson 1960), could have easily occurred. As Milne-Edwards & Grandidier (1888) listed no scops-owl for Grand Comoro, they must either have been unaware of this specimen record or dismissed it without published comment as erroneous. This anomalous record was also overlooked in the description of *pauliani* (Benson 1960). It seems improbable that typical *capnodes* occurs on Grand Comoro in sympatry with the montane *pauliani*, and even in the unlikely case of a now-extinct or overlooked lowland form occurring there, its identity with *capnodes* would seem doubly improbable given the high level of differentiation in these and other Comoran taxa. We thus presume that the locality must be erroneous.

Otus pembraensis

The Pemba Scops-Owl *Otus pembraensis* is highly distinct in many ways, although this has usually not been recognized (Pakenham 1937 and most subsequent authors, but see Pakenham 1939). It is almost unstreaked ventrally in any morph, instead being very finely vermiculated below, with broad, even rufous bands on the lower underparts (the bands coalescing in the saturated red morph); it has a 'grey' morph that is heavily rufous-washed below, and is solid rufous above; and the plumage is relatively stiff and compact. The rectal bristles and auricular extensions are very short (Table 1); the facial disk is paler, especially anteriorly, but the black disk rim is very pronounced, and a patch around the eye is very dark; the ear tufts are short and scarcely marked; the crown feathers are short; the scapulars have small white to buff scapular spots, covering only part of the outer web, and with small black tips and narrow mesial edges; the primaries are mostly plain, edged with tiny white spots and with narrow bands on the inner webs; the central rectrices and tertials are completely unbanded; the stout tarsi are very thickly feathered to well below the tarsal joint, both front and back; and the tarsal feathering is barred. The wing differs from the other taxa dealt with herein (as well as from the entire Moluccan Scops-Owl *Otus magicus* group) in having longer outer primaries (e.g., shorter primary shortfalls; Table 1). Its bill is deeper, more arched, and yellow with only the tip dark, and its claws are large and mostly pale. The downy juvenile plumage differs from those of *rutilus* and *madagascariensis* (the only other taxa of *O. rutilus* [*sensu* Marshall 1978] in which this plumage is known) in being scarcely and very vaguely barred below.

Benson (1960) remarked on the similarity of the song of *pembaensis* to that of *Otus rutilus*, but this must be taken in the context that he was comparing his own field experience (without benefit of recordings) on Mayotte and Madagascar with the brief description of vocalizations provided by Pakenham (1937). The simple, monotonous song of *pembaensis* at least superficially resembles those of Malagasy species, but the unstructured notes of c. 0.25 sec in duration are uttered singly at long and irregular intervals (NSA tape by A. Perkin; König *et al.* 1999). The nearest relative of *Otus pembaensis* is unclear but there is little or no external morphological evidence indicating this to be *rutilus*, *madagascariensis*, or any of the Comoran forms, despite tacit agreement among previous authors that *pembaensis* belongs to the *rutilus* superspecies.

Otus insularis

The Seychelles Scops-Owl *Otus insularis* has for twenty years usually been treated as a subspecies of a widespread, polytypic *O. magicus* (Marshall 1978), but this is unwarranted on morphology and biogeography (Rasmussen 1998). *Otus insularis* differs from all Malagasy and Comoran taxa in having the eartufts mostly buff with black scribbles near the tips; the short auricular feathers completely without distal extensions; the underparts very broadly streaked; the tarsi long, heavy, and feathered only at the very top; large feet; and a relatively short tail. It resembles the northern Comoran taxa, however, in having broad eartufts that are scarcely discernible among the long, fluffy head feathers. The downy fledgling of *insularis* is broadly dark-banded on a buffy background (vs. typically narrowly banded on a whitish background in *Otus magicus* ssp.). The possibility that the relationships of *insularis* are with other western Indian Ocean taxa should be reconsidered. However, no morphological characters distinguish all taxa formerly treated as races of *Otus rutilus* (sensu Marshall 1978) from the *Otus magicus* group. While the sister-species of *insularis* is unclear, its vocalizations are similar in quality only to *O. magicus* (Marshall 1978; König *et al.* 1999).

Conclusion

The vocalizations and morphology of all the *Otus* taxa from western Indian Ocean islands shows that each small-island population and the Malagasy species-pair have evolved different advertising and territorial songs that would almost certainly preclude regular interbreeding, as well as distinctive morphologies. The scops-owls of this region, despite their largely allopatric distributions, require treatment as eight separate species (*rutilus*, *madagascariensis*, *mayottensis*, *moheliensis*, *pauliani*, *capnodes*, *pembaensis*, *insularis*) under the Biological Species Concept. The taxa of the northern Comoros are well-differentiated and have probably been isolated a long time from those to the south, while the relationships of the highly distinct Pemba and Seychelles scops-owls require re-evaluation.

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References:

- Benson, C. W. 1960. The birds of the Comoro islands: results of the British Ornithologists' Union Centenary Expedition 1958. *Ibis* 103b: 5-106.
- Benson, C. W. 1999. *Type specimens of bird skins in the University Museum of Zoology, Cambridge, United Kingdom*. British Ornithologists' Club Occasional Publication No. 4, Cambridge.
- Benson, C. W., Colebrook-Robjent, J. F. R. & Williams, A. 1976. Contribution à l'ornithologie de Madagascar. *Oiseau et RFO* 46: 209-242.
- Collar, N. J. & Stuart, S. N. 1985. *Threatened birds of Africa and related islands*. The ICBP/IUCN Red Data Book, Part 1., 3rd ed. ICBP, Cambridge.
- Collar, N. J. & Tattersall, I. 1987. J. T. Last and the type-locality of Benson's Rockthrush *Monticola bensoni*. *Bull. Brit. Orn. Cl.* 107: 55-59.
- Dee, T. J. 1986. *The endemic birds of Madagascar*. ICBP, Cambridge.
- Deignan, H. G. 1961. Type specimens of birds in the United States National Museum. *Bull. U. S. N. M.* No. 221.
- Hawkins, A. F. A. 1999. Altitudinal and latitudinal distribution of east Malagasy forest bird communities. *J. Biogeogr.* 26: 447-458.
- Finsch, O. 1898. Über *Scops magicus* (S. Müll.) und die verwandten Arten. *Notes Leyden Mus.* 20: 163-184.
- Goodman, S. M., Pidgeon, M., Hawkins, A. F. A. & Schulenberg, T. S. 1997. The birds of southeastern Madagascar. *Fieldiana, Zool.* (New Ser.), No. 87.

- Grandidier, A. 1867a. Mammifères et oiseaux nouveaux découverts à Madagascar et décrits par M. Alfred Grandidier. *Rev. Mag. Zool.* (Sér. 2)19: 84-88.
- Grandidier, A. 1867b. [Letter from A. Grandidier dated 25 June 1867.] *Rev. Mag. Zool.* (Sér. 2)19: 254-256.
- Grandidier, A. 1867c. Notes sur les mammifères et les oiseaux observés à Madagascar, de 1865 à 1867. *Rev. Mag. Zool.* (Sér. 2)-19: 313-321.
- Gray, G. R. 1869. *Hand-list of genera and species of birds, distinguishing those contained in the British Museum.* Part 1, Accipitres, fissirostres, tenuirostres, and dentiostres. Trustees of the British Museum, London.
- Gurney, J. H. 1889. On an apparently undescribed species of owl from Anjouan Island, proposed to be called *Scops capnodes*. *Ibis* (Ser. 6)1: 104-107.
- Hartlaub, G. 1861. *Ornithologischer Beitrag zur Fauna Madagascar's.* Schünemann, Bremen.
- Herremans, M., Louette, M. & Stevens, J. 1991. Conservation status and vocal and morphological description of the Grand Comoro Scops Owl *Otus pauliani* Benson 1960. *Bird Conserv. Int.* 1: 123-133.
- Hornbuckle, J. 1997. Recent observations of birds in the Comoros. *Bull. Afr. Bird Cl.* 4: 43-45.
- Kaudern, W. 1922. Sauropsiden aus Madagaskar. *Zool. Jahrb.* 45: 395-458.
- Kaup, J. J. 1852. Monograph of the Strigidae. *Trans. Zool. Soc. Lond.* 4: 201-260.
- Knox, A. & Walters, M. P. 1994. *Extinct and endangered birds in the collections of the Natural History Museum.* British Ornithologists' Club Occasional Publication No. 1, London.
- König, C., Weick, F. & Becking, J. H. 1999. *Owls: a guide to the owls of the world.* Pica Press, Mountfield.
- Lafontaine, R. M. & Moolaert, N. 1998. Une nouvelle espèce de petit-duc (*Otus*, Aves) aux Comores: taxonomie et statut de conservation. *J. Afr. Zool.* 112: 163-169.
- Lewis, A. 1996. In search of the Badanga. *Bull. Afr. Bird Cl.* 3: 131.
- Lewis, A. 1998. Mayotte Scops Owl *Otus rutilus mayottensis*. *Bull. Afr. Bird. Cl.* 5: 33-34.
- Louette, M. 1988. Les oiseaux des Comores. *Ann. Koninklijk Mus. v. Midden-Afrika* (Ser. 8), No. 255.
- Marks, J. S., Cannings, R. J., Mikkola, H., Holt, D. W., Berkley, R. W., Deppe, C., Enriquez Rocha, P. L., Olsen, P. D., Petersen, J. L., Rangel Salazar, J. L., Segars, K. P. & Wood, K. L. 1999. Family Strigidae (typical owls). Pp. 76-243 in: del Hoyo, J., Elliott, A. & Sargatal, J. (eds.). *Handbook of the birds of the world.* Vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona.
- Marshall, J. T., Jr. 1978. Systematics of smaller Asian night birds based on voice. *Orn. Monogr.* No. 25. American Ornithologists' Union, Washington, D. C.
- Milne-Edwards, A. & Oustalet, E. 1888. Études sur les mammifères et les oiseaux des îles Comores. *Nouv. Arch. Mus. Hist. Nat.* (Sér. 2). Masson, Paris.
- Mittermeier, R. A., Tattersall, I., Konstant, W. R., Meyers, D. M. & Mast, R. B. 1994. *Lemurs of Madagascar.* Conserv. Int. Tropical Field Guide Ser., No. 1. Conservation International, Washington, D. C.
- Morris, P. & Hawkins, A. F. A. 1998. *Birds of Madagascar. A photographic guide.* Yale Univ. Press, New Haven.
- Pakenham, R. H. W. 1937. [Description of *Otus pembaensis*.] *Bull. Brit. Orn. Cl.* 57: 112-114.
- Pakenham, R. H. W. 1939. Field notes on the birds of Zanzibar and Pemba. *Ibis* (Ser. 14) 3: 522-554.
- Pucheran, J. 1849a. Observations sur les types peu connus du Musée de Paris. Rapaces nocturnes. *Rev. Mag. Zool.* (Jan. 1849): 17-29 (footnote).
- Pucheran, J. 1849b. Considérations générales sur les oiseaux de proie nocturnes et description de quelques espèces peu connues de cet ordre, de la collection du Musée de Paris. *Arch. Mus. Hist. Nat.* 4: 313-343.
- Rand, A. L. 1936. The distribution and habits of Madagascar birds. *Bull. Amer. Mus. Nat. Hist.* 72(5): 143-499.
- Ranf, R. D. 1995. Avisoft-Sonograph Pro 2.3 sound analysis software for Windows PCs. *Bioacoustics* 6: 253-260.
- Rasmussen, P. C. 1998. A new scops-owl from Great Nicobar Island. *Bull. Brit. Orn. Cl.* 118: 141-153.

- Safford, R. J. 1993. Rediscovery, taxonomy and conservation of the Anjouan Scops Owl *Otus capnodes* (Gurney 1889). *Bird Conserv. Int.* 3: 57-74.
- Schlegel, H. 1866. [New animals from Madagascar.] *Proc. Zool. Soc. Lond.* 1866: 419-426.
- Schlegel, H. 1873. *Revue de la collection des oiseaux de proie faisant partie du Musée des Pays-Bas. Aves noctuae. Oti.* Tome II, Monogr. 11. Brill, Leiden.
- Schlegel, H. & Pollen, F. P. L. 1868. *Recherches sur la faune de Madagascar et ses dépendences, d'après les découvertes de François P. L. Pollen et D. C. van Dam.* Pt. 2. Mammifères et oiseaux. Steenhoff, Leiden.
- Sharpe, R. B. 1870. Contributions to the ornithology of Madagascar. Part 1. *Proc. Zool. Soc. Lond.* 1870: 384-401.
- Sharpe, R. B. 1871. Contributions to the ornithology of Madagascar. Part 2. *Proc. Zool. Soc. Lond.* 1871: 313-320.
- Sharpe, R. B. 1872. Contributions to the ornithology of Madagascar. Part 3. *Proc. Zool. Soc. Lond.* 1872: 866-869.
- Sharpe, R. B. 1875a. *Catalogue of the birds of the British Museum.* Vol. II. Striges. Trustees of the British Museum, London.
- Sharpe, R. B. 1875b. Contributions to the ornithology of Madagascar. Part 4. *Proc. Zool. Soc. Lond.* 1875: 70-78.
- Sharpe, R. B. 1906. *The history of the collections contained in the Natural History Departments of the British Museum.* Vol. II. Birds. Pp. 79-515. Trustees of the British Museum, London.
- Sinclair, I. & Langrand, O. 1998. *Birds of the Indian Ocean islands.* Struik, Cape Town.
- Smith, A. 1834. African Zoology (part). *S. Afr. Quart. J.*, July-Sept.: 305-320.
- Svensson, L. 1970. *Identification guide to European passerines.* British Trust for Ornithology, Tring, U.K.
- Thompson, P. M., & Evans, M. I. 1992. The threatened birds of Ambatovaky Special Reserve, Madagascar. *Bird Conserv. Int.* 2: 221-237.
- Tristram, H. B. 1889. *Catalogue of a collection of birds belonging to H. B. Tristram, D. D., LL.D., F.R.S.* Advertiser, Durham, U.K.
- Voisin, C. & Voisin, J.-F. 1999. Liste des types d'oiseaux des collections du Muséum national d'Histoire naturelle de Paris. 6. Coucous (Cuculidae). *Zoosystema* 21: 379-402.
- Warren, R. L. M. 1966. *Type-specimens of birds in the British Museum (Natural History).* Vol. 1. Non-passerines. Trustees of the British Museum, London.
- ZICOMA. 1999. *Zones d'importance pour la conservation des oiseaux a Madagascar.* ZICOMA, Antananarivo.

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Appendix 1. Localities and coordinates for skin and fluid specimens included in analyses and mapped in Fig. 1 and 2. Localities are ordered from north to south on the west side of Madagascar, then from north to south on the east. For some localities, adult specimens were not studied, and thus they do not appear in the summary statistics. Under 'Remarks', citations in parentheses are published, while those without are collectors and year of collection.

Site No	Name	Coordinates	Remarks
1	Anaborano	13°32'S, 48°50'E	'western in character' (Rand 1936)
2	Mahajunga/Bombetoka	15°43'S, 46°19'E / 15°50'S, 46°15'E	?/van Dam 1870
3	Anaboratabe	c. 16°00'S, 46°05'E	valley with palms and deciduous forest (Rand 1936)
4	Namaroka	16°05'S, 45°21'E	gallery and deciduous plains forest (Rand 1936)
5	Andranolava	16°10'S, 47°58'E	(Kaudern 1922)
6	Tsiandro	18°42'S, 44°53'E	scattered trees, some heavy hill forest (Rand 1936)
7	Morondava	20°19'S, 44°17'E	van Dam 1871
8	Ankasoabo/Tabiky	22°17'S, 44°31'E	Ljungqvist 1929
9	3 h N Ivohibe	22°28'S, 46°53'E	Ankerana, forest edge (Rand 1936)
10	Anavelona	22°40'S, 44°11'E	Goodman 1999 (pers. comm.)
11	Sakaraha/Zombitsy	22°54'S, 44°31'E/ 22°51'S, 44°43'E	song a harsh, guttural 'k-r-r-r-k' in a series of 4-5 (Benson <i>et al.</i> 1976)/ edge of savannah & wet-dry forest, Goodman 1993
12	Sarodrano	23°31'S, 43°45'E	'scrub at base of cliffs', Peterson <i>et al.</i> 1967
13	Antinosy	c. 23°25'S, 44°45'E	J. T. Last (Collar & Tattersall 1987); not 'Loast' as on AMNH specimen labels
14	Lac Tsimanampetsotsa	24°08'S, 43°45'E	one found in a limestone cave (Rand 1936)
15	Amboasary	25°10'S, 46°15'E	Bluntschli 1931
16	Mt. des Francais	c. 12°40', c. 49°00'	Melou 1917 (not precisely located)
17	Nosy Be	13°20'S, 48°15'E	Grandidier 1866-67
18	Ambodavy/ Pasandava Bay	c. 13°40'S, 48°15'E / c. 13°40'S, 48°15'E	= Ampasindava; see Collar & Stuart (1985)
19	1 day S Anaborano	c. 13°32'S, 48°50'E	in humid evergreen forest (Rand 1936)
20	Antanambao	14°01'S, 48°25'E	Goodman 1999 (pers. comm.)
21	1 day E Maromandia	c. 14°13'S, 48°05'E	both forest and non-forest in area (Rand 1936)
22	1 day W Andapa	c. 14°39', 49°40'E	mountain forest and open areas (Rand 1936)
23	Andapa	14°39', 49°40'E	brush and mountain forest (Rand 1936)
24	near Maroantsetra	15°23'S, 49°44'E	heavy forest (Rand 1936)
25	Mahambo	17°29'S, 49°28'E	Newton 1865
26	Sianaka	c. 18°S, 49°E	Herschell-Chauvin 1925-7, Devolle 1949-52
27	Didy	c. 18°05'S, 48°30'E	Deignan 1962
28	Beforona /Rogez/ Périnet/Imerina	18°58'S, 48°35'E/ 18°48'S, 48°37'E	Lamberton 1922-23; Benson, Wills 1892-96

		18°56'S, 48°25'E/ c. 19°00'S, 48°00'E (last site not precisely located)	
29	c. 43 km S Ambalavao	22°13'S, 47°00'E	Goodman 1993
30	30 km W Vondrozo	22°50'S, 47°20'E	FAA 1929
31	Marosohy Forest	24°34'S, 46°48'E	closed-canopy forest, Goodman 1989
32	Mandena Forest	24°58'S, 47°01'E	littoral forest, Schulenberg 1989
33	near Tolagnaro (Ft. Dauphin)	c. 25°02'S, 46°00'E / 24°59'S, 46°56'E	Milon 1948/ Goodman 1990

Appendix 2. Localities and coordinates for vocalizations included in analyses, ordered as for Appendix 1. Summary statistics were analysed from means for each individual tape cut, so number of phrases per individual is number of replicates for each.

Site No.	Name	Coordinates	Analysis by:	Species	No. phrases/ individual
1	Nosy Be	13° 20'S, 48° 15'E	RV	<i>madagascariensis</i>	6
2	Karambao	16° 13'S, 46° 56'E	TSS	<i>madagascariensis</i>	5
3	Ampijoroa	16° 15'S, 46° 48'E	TSS, RV	<i>madagascariensis</i>	6, 10
4	Ankorokaroka	16° 16'S, 47° 03'E	TSS	<i>madagascariensis</i>	5
5	Namoroka	16° 05'S, 45° 21'E	RV	<i>madagascariensis</i>	11
6	Analamaintso	18° 20'S, 47° 07'E	RV	<i>madagascariensis</i>	6
7	Tsimembo	18° 13-19° 07'S, 44° 34-57'E	RV	<i>madagascariensis</i>	9
8	Ihosy	22° 24'S, 46° 07'E	TSS	<i>madagascariensis</i>	8
9	Isalo	22° 33'S, 44° 23'E	RV	<i>madagascariensis</i>	5
10	Zombitse	22° 48'S, 44° 40'E	TSS, RV	<i>madagascariensis</i>	5, 7
11	Ifaty	23° 06'S, 43° 37'E	TSS	<i>madagascariensis</i>	5
12	Andohahela Parcel 2	c. 24° 48'S, 46° 30'E	RV	<i>madagascariensis</i>	5
13	Hazofotsy	24° 49'S, 46° 33'E	TSS	<i>madagascariensis</i>	7, 8
14	Berenty	c. 24° 59'S, 46° 17'E	TSS	<i>madagascariensis</i>	5, 6, 6
15	Hiaraka	15° 29'S, 49° 56'E	TSS	<i>rutilus</i>	5
16	Ambanizana	15° 41'S, 49° 57'E	TSS	<i>rutilus</i>	5
17	Kalotsara	17° 42'S, 48° 46'E	TSS	<i>rutilus</i>	7
18	Rangovaloa	c. 17° 26-44'S, 48° 56-59'E	RV	<i>rutilus</i>	6
19	Maninilaza	c. 17° 26-44'S, 48° 56-59'E	RV	<i>rutilus</i>	5
20	Reserve Speciale d'Analamazaotra (Périnet)	18° 28'S, 48° 28'E	TSS, RV	<i>rutilus</i>	5, 5, 7
21	Parc National Ranomafana	21° 16'S, 47° 26'E	TSS	<i>rutilus</i>	5, 4
22	Manombo	23° 02'S, 47° 44'E	TSS	<i>rutilus</i>	5, 6
23	Andohalela Parcel 1	c. 24° 36'S, 46° 42'E	RV	<i>rutilus</i>	8
24	Mandena Forest	24° 58'S, 47° 01'E	TSS	<i>rutilus</i>	11, 7, 7, 7